



# Toward a theory of topopatric speciation: The role of genetic assortative mating



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## HIGHLIGHTS

- We derive the equations for the haplotype frequencies under assortative mating.
- We find equilibrium solutions and study their stability.
- Equilibria are characterized by the disappearing of one allele.
- We study times of convergence to equilibria.
- Certain combination of allele frequencies remains constant throughout the dynamics.

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## ABSTRACT

We discuss a minimalist model of assortative mating for sexually reproducing haploid individuals with two biallelic loci. Assortativeness is introduced in the model by preventing mating between individuals whose alleles differ at both loci. Using methods of dynamical systems and population genetics we provide a full description of the evolution of the system for the case of very large populations. We derive the equations governing the evolution of haplotype frequencies and study the equilibrium solutions, stability, and speed of convergence to equilibrium. We find a constant of motion which allows us to introduce a geometrical construction that makes it straightforward to predict the fate of initial conditions. Finally, we discuss the consequences of this class of assortative mating models, including their possible extensions and implications for sympatric and topopatric speciation.

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## 1. Introduction

While the origin of species has always been a central subject in evolutionary biology, the large number of recent empirical and theoretical developments has renewed the interest in the area [1–4]. Among the vast body of literature, individual-based simulations have shown to be specially important in fostering relevant discussions in speciation [5–17]. Within this class we find a neutral model of speciation formulated by de Aguiar and coworkers, which successfully predicts empirical patterns of species diversity [13]. Simulations of the model demonstrate that even in the absence of natural selection speciation can

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occur as a consequence of two reinforcing trends: isolation mediated by spatial distance and isolation mediated by genetic incompatibility. Originally studied by Sewall Wright in 1943 [18], isolation by spatial distance involves a physical mating restriction modeled through a parameter  $S$ , representing the search radius for the individuals to find a potential partner. Isolation by genetic incompatibility, on the other hand, is included in the model by preventing mating between individuals whose genetic distance (defined as the number of loci displaying different alleles) exceeds a maximum tolerable difference of  $G$ . The latter scheme of assortativeness was introduced by Higgs and Derrida [5], and is motivated by the fact that mate choice often relies on multiple cues that are determined genetically [19].

As speciation in this context occurs in a single non-panmictic population, the model could be considered parapatric [20]. However, the geographical context of speciation is usually defined in terms of the ranges of the initial populations or the amount of gene flow between different demes. In this case, populations are said to be parapatric when the initial allelic exchange rate is neither zero nor maximum [2]. Even though this definition of parapatry is very broad and turns sympatry and allopatry into limiting cases, it still does not describe precisely the scenario adopted by the model of Aguiar and coworkers. Since individuals have to be sufficiently close to each other in space to reproduce, there is an explicit mechanism acting on the individuals that leads to a spatially structured population and isolation by distance. There are no predefined population ranges: ranges develop spontaneously during the evolution of an initially uniformly distributed population. It resembles a ferromagnetic phase transition, in the course of which a symmetry is broken leading to the formation of quasi-homogeneous clusters [21]. In the present framework, the clusters correspond precisely to species. Therefore, to emphasize the spatial mechanism that does not rely on assumptions about the range of the nascent species the term topopatry was adopted.

In this paper we give a first step in the construction of a population genetics theory for topopatric speciation by considering the simplest example in which the effect of assortative mating may be implemented. Specifically, we analyze the dynamics of a population of haploid and hermaphrodite individuals bearing only two biallelic loci. We further assume that sexual reproduction is possible between individuals whose haplotypes differ in at most one locus, i.e., the maximum allowed genetic distance is  $G = 1$ . We perform a detailed examination of the dynamics of haplotype and allele frequencies for the case of an infinitely large population with no mutations.

The paper is organized as follows: in Section 2 we describe a general reproductive mechanism that allows for the construction of different mating models, including assortativeness based on genetic compatibility. In Section 3 we briefly consider the case of random mating. Evolution under assortative mating is analyzed in Section 4, including the description of equilibria and their stability, rates of convergence, and constants of motion. Finally, in Section 5 we expose our conclusions and discuss the possible consequences of our results for the sympatric and topopatric speciations. Auxiliary mathematical material is included in appendices.

## 2. Reproductive model

Consider a population of hermaphrodite individuals with haploid genomes consisting of two biallelic loci. The state of the population in the generation  $t$  can be specified by the number of individuals having each of the four possible haplotypes,  $AB$ ,  $Ab$ ,  $aB$ , and  $ab$ , where  $A$  and  $a$  are the alleles at one locus, and  $B$  and  $b$  the alleles at the other. These numbers are denoted by  $N_{AB}^t$ ,  $N_{Ab}^t$ ,  $N_{aB}^t$  and  $N_{ab}^t$ , with  $N_{AB}^t + N_{Ab}^t + N_{aB}^t + N_{ab}^t = N^t$ , the total size of the population. Encounters between the members of this generation may succeed or not in producing offspring for the generation  $t + 1$ , depending on the probabilities  $w_{h_1;h_2}$  ( $h_1$  and  $h_2$  being the parental haplotypes). The rates  $w_{h_1;h_2}$  (see Table 1) incorporate both the effects of the compatibility between the parents (sexual selection) and the viability of the newly formed zygote (viability selection). In our model the viability selection is the same for all individuals, and takes place once the zygote was formed through the inheritance of a recombinated chromosome (the recombination of the parental chromosomes occurs at a recombination rate  $r$ ). Assortativeness, represented by the sexual selection component, is described by the compatibility between the parents and acts at a prezygotic level. The reason for adding a postzygotic factor to the compound fitness  $w_{h_1;h_2}$ , from now on the compatibility–viability selection rate, has the only purpose of keeping the total number of individuals constant across generations, and represents an implicit carrying capacity, i.e., finite abundance of resources.

According to Table 1, and assuming non-overlapping generations, the number of  $AB$  individuals in the generation  $t + 1$  obeys

$$N_{AB}^{t+1} = \frac{1}{2}N_{AB}^t(N_{AB}^t - 1)w_{AB:AB} + \frac{1}{2}N_{AB}^tN_{Ab}^tw_{AB:Ab} + \frac{1}{2}N_{AB}^tN_{aB}^tw_{AB:aB} + \frac{r}{2}N_{AB}^tN_{ab}^tw_{AB:ab} + \frac{1-r}{2}N_{Ab}^tN_{aB}^tw_{Ab:aB}. \quad (1)$$

The evolution equations for the other haplotypes can be obtained similarly:

$$N_{Ab}^{t+1} = \frac{1}{2}N_{Ab}^t(N_{Ab}^t - 1)w_{Ab:Ab} + \frac{1}{2}N_{AB}^tN_{Ab}^tw_{AB:Ab} + \frac{1}{2}N_{Ab}^tN_{aB}^tw_{Ab:aB} + \frac{r}{2}N_{AB}^tN_{ab}^tw_{AB:ab} + \frac{1-r}{2}N_{Ab}^tN_{aB}^tw_{Ab:aB} \quad (2)$$

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